



Visual perception and visual mental imagery of emotional faces generate similar expression aftereffects



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ABSTRACT

What is the relationship between visual perception and visual mental imagery of emotional faces? We investigated this question using a within-emotion perceptual adaptation paradigm in which adaptation to a strong version of an expression was paired with a test face displaying a weak version of the same emotion category. We predicted that within-emotion adaptation to perception and imagery of expressions would generate similar aftereffects, biasing perception of weak emotional test faces toward a more neutral value. Our findings confirmed this prediction. Adaptation to mental images yielded aftereffects that inhibited emotion recognition of test expressions, as participants were less accurate at recognising these stimuli compared to baseline. While the same inhibitory effect was observed when expressions were visually perceived, the size of the aftereffects was greater for perception than imagery. These findings suggest the existence of expression-selective neural mechanisms that subserve both visual perception and visual mental imagery of emotional faces.

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1. Introduction

An encounter with a familiar person's name is often all we need to experience a mental image of that person's face. Visual mental imagery is the process by which neural representations of visual stimuli are retrieved from long-term memory and maintained in working memory (e.g. [Kosslyn, Thompson, & Ganis, 2006](#)). A prominent theory (image-percept equivalence theory) claims that visual mental imagery activates the same neural mechanisms involved in visual perception (e.g. [Kosslyn et al., 2006](#)). Several studies support this claim by showing that visual mental imagery activates brain mechanisms involved in visual perception, including retinotopically mapped areas of the visual cortex (e.g. [Slotnick, Thompson, & Kosslyn, 2005](#)) and motion-selective cortical regions (e.g. [Grossman & Blake, 2001](#)). Mental imagery has also been shown to activate neural sites involved in visual perception of complex stimuli such as faces. For example, [O'Craven and Kanwisher \(2000\)](#) observed that a portion of the fusiform face area (FFA), which is usually active during perception of faces, is also active when faces are visually imagined. Further evidence that perception and imagery of faces recruits similar neural mechanisms comes from studies of patients with prosopagnosia, showing that impairments in face recognition often correlate with deficits in face imagery (e.g. [Young, Humphreys, Riddoch, Hellowell, & de Haan, 1994](#)).

Although the image-percept equivalence theory does not claim that visual perception and imagery are identical in every respect, it predicts that some psychophysical effects observed during perception of visual stimuli should also occur when

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these stimuli are merely imagined (Kosslyn et al., 2006). It should therefore be possible to use psychophysical methods to investigate the neural mechanisms underlying visual perception and imagery. One such method involves the use of selective adaptation paradigms in which prolonged exposure to an adapting stimulus causes temporary perceptual distortions, known as adaptation aftereffects (e.g. Koehler & Wallach, 1944). Adaptation paradigms provide information about the neural underpinnings of perceptual experience through changes to the appearance of stimuli following an extended period of exposure to another stimulus. In the waterfall effect, for example, prolonged exposure to the downward motion of the water induces an imbalance in the response properties of direction-selective neurons, leading to a bias to perceive the opposite stimulus property (i.e. upward motion). This bias generates an aftereffect in which a stationary object seems to move upwards. The waterfall aftereffect therefore provides indirect evidence for the existence of direction-selective neural mechanisms.

Adaptation aftereffects are not limited to low-level visual properties. Recent studies have reported aftereffects for high-level facial attributes such as identity (e.g. Leopold, O'Toole, Vetter, & Blanz, 2001), gender (e.g. Webster, Kaping, Mizokami, & Duhamel, 2004), ethnicity (e.g. Jaquet, Rhodes, & Hayward, 2007), age (e.g. O'Neil & Webster, 2011), gaze direction (e.g. Jenkins, Beaver, & Calder, 2006) and expression (e.g. Webster et al., 2004). In recent years, adaptation paradigms have also been used to study the effect of visual mental imagery on perception of facial identity (Hills, Elward, & Lewis, 2008, 2010; Ryu, Borrmann, & Chaudhuri, 2008) and gender (DeBruine, Welling, Jones, & Little, 2010; D'Ascenzo, Tommasi, & Laeng, 2014; Zamuner, Oxner, & Hayward, 2016). Despite this renewed interest in visual mental imagery, researchers have not yet investigated adaptation to imagery of facial expressions. The present work is therefore the first study to examine expression aftereffects following perception and imagery of emotional faces.

Previous research has reported expression aftereffects following perceptual adaptation to emotional faces. In an early study, Hsu and Young (2004) investigated adaptation to expressions of fear, happiness and sadness. Results showed that when the adapting and test expressions were from the same emotion category (within-emotion adaptation), perception was biased away from the test category. This perceptual shift had an inhibitory effect on the recognition of test expressions. For example, adaptation to a sad face decreased the likelihood that participants would rate a neutral-sad test expression as sad. By contrast, a facilitatory effect was sometimes observed when the adapting and test stimuli were from different emotion categories (cross-emotion adaptation), as adaptation to a sad face increased the likelihood that participants would rate a neutral-happy test expression as happy. More recently, Rutherford, Chattha, and Krysko (2008) reported that adaptation to negative expressions (anger, disgust, fear and sadness) caused neutral test stimuli to appear happy, whereas adaptation to expressions of happiness biased perception in the opposite direction. Pell and Richards (2011) further investigated adaptation to expressions of anger, disgust, and fear. Consistent with evidence from Hsu and Young (2004), within-emotion adaptation had an inhibitory effect on emotion recognition. Specifically, adaptation to expressions of anger and disgust biased perception away from the test stimulus, when this was an intermediate morph between the adaptor and a neutral face. However, in contrast with Hsu and Young's observation, cross-emotion adaptation did not consistently yield a facilitatory effect on emotion recognition. While adaptation to fear facilitated recognition of neutral-disgusted expressions, adaptation to disgust had an inhibitory effect on the recognition of neutral-angry stimuli. Interestingly, adaptation to anger had no effect on the recognition of intermediate morphs between neutral and disgusted.

In the present study, we used a within-emotion perceptual adaptation paradigm to investigate whether perception and imagery of emotional faces generate similar aftereffects. Prototype facial expressions of the six basic emotions, both viewed and imagined, were used as adapting stimuli. Visually presented faces displaying expressions half the intensity of the adaptors were used as test stimuli. We investigated adaptation by measuring the effect that prolonged exposure to prototype expressions had on the recognition of test stimuli. Previous research (Hsu & Young, 2004) has shown that within-emotion perceptual adaptation to prototype expressions can inhibit the recognition of neutral-emotional test faces. Specifically, Hsu and Young observed that within-emotion adaptation decreased the likelihood that participants would recognise weak test expressions compared to when participants were adapted to a baseline stimulus made of black dots. If mental imagery of emotional faces recruits many of the same neural mechanisms responsible for perceptual adaptation, then within-emotion adaptation to mental images of prototype expressions will cause a similar inhibitory effect. Thus, we predicted that participants would be less accurate at recognising test expressions compared to baseline. However, a major difference between Hsu and Young's design and ours was that, in the present study, baseline ratings were acquired in a separate categorisation task in which participants rated the emotional appearance of the same expressions that were used as test stimuli for the perception and imagery tasks. We will return to this issue in the Discussion.

To test our prediction, we had participants perform three separate tasks: baseline, perception and imagery. The order of these tasks was counterbalanced across participants. The baseline task involved rating the emotional appearance of test faces. In the perception and imagery tasks, the same faces were rated following adaptation to perception and imagery of prototype expressions. For the imagery task, all participants memorised six adaptors, each one showing the same face with a different expression. During the adapting phase of the imagery task, participants recalled and visualised these expressions. The same adaptors were used for the perception task. Only one identity was therefore viewed and imagined throughout the entire experiment. This feature of our design was aimed at minimising effort during encoding, storage and retrieval of the six adaptors, and at maximising the accuracy of the corresponding mental images. The differences in mean ratings between baseline, perception and imagery tasks were used to infer the direction and magnitude of the aftereffects.

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